CHROMOSOME CYTOLOGY OF IRIDACEAE—PATTERNS OF VARIATION, DETERMINATION OF ANCESTRAL BASE NUMBERS, AND MODES OF KARYOTYPE CHANGE[1]

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ABSTRACT

Against a background of 100 original counts for 95 species in 34 genera of Iridaceae, we review chromosome information for the entire family. Counts are now available for some 1008 of the estimated 1750 species of Iridaceae, and all but 5 of ca. 78 genera are known from at least one count. We suggest ancestral base numbers for all genera known cytologically and outline patterns of cytological variation within the subfamilies and tribes currently recognized. Polyploidy was evidently important in the early diversification of Iridaceae, and many genera have base numbers higher than $x = 10$. Neopolyploidy is important in Northern Hemisphere genera, especially *Iris* and *Crocus*, but has an unusually low frequency in Africa, the center of diversity for the family. Changes in basic number, frequent in a few genera, are evidently the result of dysploid reduction. In all but a few possible examples, correlated morphological specialization suggests that dysploid reduction is involved in stepwise change in base number. Major dysploid series are restricted to a few genera, including *Romulea*, the related *Crocus*, as well as *Gladiolus* and *Lapeirousia* (all Ixioideae), and *Iris*, *Moraea*, and *Sisyrinchium* (Iridoideae). All other genera have a single base number or limited variation evident in only one or two species. Patterns of chromosomal variation are particularly complex in *Iris* and *Crocus* and await detailed elucidation. More counts are needed in the Australian *Patersonia*, the South American-Australasian *Orthrosanthus*, and the neotropical tribe Mariceae, for all of which ancestral base number remains uncertain and patterns of cytological variation appear complex.

Chromosome cytology in the petaloid monocot family Iridaceae is unusually varied in features of the karyotype including basic number, ploidy level, overall size, and chromosome arm ratios. It is thus an important factor in considerations of the systematics and evolution of this family of some 1750 species in ca. 78 genera (Goldblatt, 1990a, 1991). Iridaceae are consequently comparatively well known chromosomally. Including several new counts published here for a range of genera and species, some until now poorly or not at all known cytologically, there are now counts available for at least half the species in the family, including a good sampling of three of the four subfamilies currently recognized: Nivenioideae, Iridoideae, and Ixioideae. The fourth subfamily, Isophysidoideae, which is monotypic, remains uncounted, an unfortunate gap in our knowledge because this taxon appears to occupy a basal or near basal position in the family (Goldblatt, 1990a; Chase et al., 1995 and unpublished). Ancestral chromosome numbers can be suggested for almost all genera, and patterns of chromosomal variation within genera, and sometimes among related genera, now seem to be reasonably well understood.

Here, patterns of chromosomal variation are interpreted against a background of the systematics and morphology of the Iridaceae. We also draw attention to those genera that are uncounted or poorly known and require further investigation in order to interpret the variation in their karyology. As part of our review of chromosome number and morphology of the family, we also review the available data on genome size.

Methods used are described elsewhere (Goldblatt, 1990a; Goldblatt et al., 1993; Goldblatt & Takei, 1993) and invariably involved squashes of root tips or shoot apices, pretreated in a variety of ways.

RESULTS

Original counts are presented in Table 1, accompanied by voucher information. Karyotypes are not described individually; instead, results are illustrated and notable karyotypic details are described under Discussion.

DISCUSSION

PATTERNS OF VARIATION AND DETERMINATION OF ANCESTRAL BASE NUMBERS

1. NIVENIOIDEAE

This relatively primitive subfamily of six genera and ca. 85 species (Table 2) consists of the large African and Madagascan *Aristea*, the Madagascan saprophyte, *Geosiris*, three shrubby southern African genera, and the Australasian *Patersonia*. Derived features of the subfamily (Manning & Goldblatt, 1991) are a binate rhipidial inflorescence, a blue perianth that is fugacious and deliquescent in some genera, and a 2–3-seriate outer seed integument. *Aristea* and the shrubby southern African *Klattia*, *Nivenia*, and *Witsenia* have a common base number, $x = 16$ (Table 2), and small chromosomes (Figs. 1–5) with a size range 0.8–2.5 μm. *Patersonia* is inadequately sampled (Goldblatt, 1979a) and also has small chromosomes (Fig. 6), comparable in size to those of *Aristea*. Diploid numbers of $2n = 62, 42$, and 22, the latter the most frequent, have been reported in the 6 species of *Patersonia* counted out of a total of 20 in the genus. From these counts we assume the most likely ancestral base number for *Patersonia* may be $x = 11$. It seems premature to speculate about how the base number in *Patersonia* relates to $x = 16$ in the remaining genera of Nivenioideae. *Patersonia* has been suggested to be nested within Nivenioideae and to be the sister genus to the lineage that includes *Nivenia*, *Klattia*, and *Witsenia* (Manning & Goldblatt, 1991). If $x = 11$ is correct, then ancestral base number in *Patersonia* must be derived. Additional counts in the genus are needed before the situation here is clarified. *Geosiris* is unknown cytologically.

2. IRIDOIDEAE

Iridoideae share with Ixioideae specialized xylem vessels in the roots with simple perforations, likely a specialized condition (Cheadle, 1963; Goldblatt et al., 1987), similar and putatively derived anther endothecial thickenings (Manning & Goldblatt, 1990), and a more specialized spectrum of flavonoid compounds than in Nivenioideae (Goldblatt, 1990a). Possibly a clade, Ixioideae and

Iridoideae, nevertheless, differ considerably in many features, including pollen grain morphology, leaf anatomy, and inflorescence structure (Goldblatt, 1990a, Goldblatt et al., 1991). Iridoideae are defined largely by a fugacious perianth and hollow, terminally stigmatic styles that divide below the anthers. These two morphological synapomorphies are supported by the presence of an unusual chemical character, free meta-carboxy amino acids (Goldblatt, 1990a), not present elsewhere in the family. In three of the four tribes of Iridoideae the style branches are further specialized in being thickened or compressed, and the apices are elaborated into crests or similar structures (Goldblatt, 1990a; Rudall, 1994).

Of the four tribes (Table 2), Sisyrinchieae are basal, while the remaining Irideae, Mariceae, and Tigridieae may be a monophyletic lineage defined by several morphological and chemical synapomorphies (Goldblatt, 1990a). Chromosomes of many Sisyrinchieae, including *Libertia* and *Orthrosanthus*, are small, generally 1–2 μm long (Figs. 7–9), and comparable in size to those of Nivenioideae. In *Sisyrinchium*, the largest genus of the tribe, the chromosomes are usually somewhat larger (Kenton & Heywood, 1984), sometimes substantially so in *Olsynium* (Kenton et al., 1987, reported as *Phaiophleps* and *Sisyrinchium* sections *Eriphilema* and *Nuno*). *Bobartia*, usually regarded as the only African genus of Sisyrinchieae, has been transferred to Irideae as a result of molecular data (Souza-Chies et al., 1997). Its comparatively large chromosomes and $x = 10$ match the plesiomorphic features of the latter tribe.

Basic chromosome number in *Libertia* is evidently $x = 19$, established for four Australasian species (Hair et al., 1967), but the only South American species counted has $2n = $ ca. 72 (Kenton & Heywood, 1984), making this possibly tetraploid if it, too, is based on $x = 19$. Base number for *Libertia* in South America still needs to be verified. In the only other American and Australasian genus of Iridaceae, *Orthrosanthus*, base number is uncertain. We have established $2n = 84$ in the Australian *O. polystachyus* (Fig. 7), also reported as $2n = 40$ (Kenton & Heywood, 1984). In the South American *O. chimboracensis* and *O. acorifolius* (Figs. 8–9) we found $2n = 54$. This accords with an earlier count of $n = 27$ for *O. chimboracensis*, based on a different collection (Goldblatt, 1982a). Kenton and Heywood (1984), however, have reported $2n = 50$ in both *O. chimboracensis* and *O. exsertus* (as var. *exsertus*). The difference in the counts seems to concern the identity of four small chromatin bodies, regarded as satellites by Kenton and Heywood, but

Table 1. New chromosome numbers in Iridaceae (Figs. 1–46) with collection data. Unless stated to the contrary, vouchers are at the Missouri Botanical Garden (MO)—herbarium acronyms are abbreviated according to Holmgren et al. (1981) and are indicated in parentheses after the collection number. Species are arranged alphabetically within the subfamilies and tribes recognized by Goldblatt (1990a).

Species	Diploid number 2n	Collection data
Subfamily Nivenioideae		
Aristea abyssinica Pax	64	Zimbabwe, Nyanga, *Goldblatt 9070*
A. anceps Eckl. ex Klatt	32	S. Africa, E. Cape, near Fish R. mouth, *Goldblatt 9053*
A. angolensis Baker	32	Malawi, Zomba Mt., *Goldblatt 4528*
A. juncifolia Baker	32	S. Africa, W. Cape, Cape Point Reserve, *Goldblatt 9056*
A. angustifolia Baker	32	Madagascar, Andringitra, *Goldblatt 8971*
Patersonia sericea R. Br. ex Ker Gawl.	22	Australia, NSW, Clarence, *Hind 693* (NSW)
Subfamily Iridoideae		
Tribe Irideae		
Barnardiella spiralis (N.E. Br.) Goldblatt	20	S. Africa, N. Cape, Richtersveld, *Viviers s.n.*
Dietes robinsoniana (F. Muell.) Klatt	60	Lord Howe Island, *Pickard 3377* (NSW)
Ferraria glutinosa (Baker) Rendle	40	Namibia, near Rehoboth, *Goldblatt & Manning 8808*
Iris tridentata Pursh	40	U.S.A., Florida, Leon Co., *Henderson 92-135*
Homeria hantamensis Goldblatt & J. C. Manning	12	S. Africa, N. Cape, Hantamsberg, *Goldblatt & Manning 10355*
Moraea anomala G. J. Lewis	20	S. Africa, W. Cape, Elim, *Goldblatt 361* (BOL)
M. bella Harms	12	Tanzania, Ufipa, *Goldblatt et al. 8289*
M. bipartita L. Bolus	12	S. Africa, W. Cape, *Goldblatt 4948*
M. callista Goldblatt	12	Tanzania, Kitulo Plateau, *Lovett & Congdon 2905*; Lusitu Ridge, Njombe, *Spurrier s.n.* (no voucher)
M. carsonii Baker	12	Zambia, Copperbelt, *Goldblatt 7544*
M. deserticola Goldblatt	12	S. Africa, N. Cape, Knersvlakte, *Goldblatt 9128*
M. elsiae Goldblatt	20	S. Africa, W. Cape, Kenilworth, *Esterhuysen 32358* (BOL)
M. fergusoniae L. Bolus	12	S. Africa, W. Cape, Caledon district, *Snijman 820* (NGB); Mierkraal, Bredasdorp, *Goldblatt 6186*; E. of Heidelberg, *Goldblatt 4956*; Bontebok Park road, *Goldblatt 4316A*
M. fugax (D. Delaroche) Ker Gawl.	10	S. Africa, N. Cape, Wallekraal, *Goldblatt s.n.* (no voucher)
M. incurva G. J. Lewis	12	S. Africa, W. Cape, near Tulbagh, *Hansford 1* (NBG)
M. namibensis Goldblatt	20	Namibia, Süd Witputs, *Lavranos 21257*
M. neglecta G. J. Lewis	20	S. Africa, W. Cape, Klaasjagersberg, *Goldblatt 5268*
M. tulbaghensis L. Bolus	12	S. Africa, W. Cape, near Tulbagh, *Burgers 2756* (STE)
M. schimperi (Hochst.) Pic. Serm.	12	Zaire, Shaba, *Schaijes 5108*
M. unguiculata Ker Gawl.	12	S. Africa, W. Cape, *Goldblatt 5865*
Tribe *Mariceae*		
Neomarica caerulea (Ker Gawl.) Sprague	32	ex hort., origin unknown, *Goldblatt 5930*
N. cf. *northiana* (Schneev.) Sprague	18	Paraguay, Amambay, Cerro Corá, *Solomon et al. 6950*
Trimezia martinicensis (Jacq.) Herb.	80	Venezuela, Anzoátegui, Serranía de Turimiquire, *Davidse & González 19456*; Venezuela, Mérida, Páramo de Mucubaji, *Berry 3802*
Tribe Sisyrinchieae		
Orthrosanthus polystachyus Benth.	84	Australia, ex Hort. Bot. Melbourne, *Goldblatt s.n.*

Table 1. Continued.

Species	Diploid number $2n$	Collection data
O. acorifolius (Kunth) Ravenna	54	Venezuela, Mérida, *Grifo & Hahn 361* (BH)
O. chimboracensis (Kunth) Baker	54	Venezuela, *Dorr et al. 5044* (NY)
Sisyrinchium micranthum Cav.	48	Nicaragua, *Henrich s.n.*
Tribe Tigridieae		
Alophia drummondii (Graham) R. C. Foster	28	U.S.A., Texas, Bastrop Co., *Lee* sub *Goldblatt s.n.*
Calydorea azurea Klatt	28	Uruguay, Treinta y Tres to Tacuarembó, *Castillo 1146* sub *Goldblatt s.n.*
C. amabilis (Ravenna) Goldblatt & Henrich	14	Argentina, Entre Ríos, Concepción del Uruguay, *Goldblatt s.n.*
C. pallens Griseb.	28	Argentina, Córdoba, Cerro Colorado, *Goldblatt s.n.*
C. xiphioides (Poepp.) Espinosa	42	Chile, Coquimbo, *Hoffmann s.n.*
Cipura paludosa Aubl.	14	Brazil, Maranhao, near Imperatriz, *Plowman et al. 9305*
Cobana guatemalensis (Standl.) Ravenna	28	Honduras, *Nelson s.n.* (no voucher)
Cypella fucata Ravenna	14	Uruguay, Maldonado, Punta del Este, *Castillo s.n.*
C. herbertii subsp. *brevicristata* Ravenna	14	Uruguay, Artigas, northern suburbs, *Castillo s.n.* (no voucher)
subsp. *wolfheugelii* (Hauman) Ravenna	14	Argentina, Buenos Aires, Cerro Ventana, *Lamberto & Möchel s.n.* (BB 3881)
C. hauthalii subsp. *opalina* Ravenna	14	Argentina, Misiones, Garruchos, *Castillo s.n.* (FAA)
Ennealophus euryandrus (Griseb.) Ravenna	14	Bolivia, Tarija, Arce, *Solomon 9972*
E. foliosus (Kunth) Ravenna	14	Peru, *Dillon 4514* (F)
Herbertia lahue Molina	42	Chile, *Ornduff 9153* (UC); U.S.A., Louisiana, Shreveport, *Heikamp, s.n.*
H. aff. *lahue*	14	Brazil, Rio Grande do Sul, Rosario do Sul, *Castillo s.n.*
H. pulchella Sweet	42	Uruguay, Maldonado, Punta del Este, *Castillo* sub *Goldblatt s.n.*
H. quareimana Ravenna	28	Brazil, Rio Grande do Sul, Uruguaiana, *Goldblatt s.n.*
Subfamily Ixioideae		
Tribe Watsonieae		
Micranthus junceus (Baker) N.E. Br.	20	S. Africa, W. Cape, Cape Point Reserve, *Goldblatt s.n.* (no voucher)
Thereianthus spicatus var. *linearifolius* G. J. Lewis	20	S. Africa, W. Cape, Cape Point, *Goldblatt 5400*
Watsonia dubia Eckl. ex Klatt	18	S. Africa, W. Cape, Malmesbury, *Goldblatt 8708*
W. hysterantha Mathews & L. Bolus	18 + 1B	S. Africa, W. Cape, Langebaan, *Snijman 71* (BG)
W. minima Goldblatt	18	S. Africa, W. Cape, near Greyton, *Goldblatt 8047*
Tribe Ixieae		
Crocus longiflorus Raf.	28	Italy, Sicily, Eloro, *Goldblatt 5073*
Dierama inyangense Hilliard	20	Zimbabwe, Nyanga, *Clarke s.n.* (no voucher)
Geissorhiza callista Goldblatt	26	S. Africa, W. Cape, near Grayton, *Goldblatt 8680*
G. foliosa Baker	26	S. Africa, W. Cape, Strawberry Hill, *Goldblatt 7948*
G. roseoalba (G. J. Lewis) Goldblatt	26	S. Africa, E. Cape, Pootjeshoogte, *Vlok 1663*
Gladiolus aquamontanus Goldblatt & Vlok	30	S. Africa, W. Cape, Rust-en-Vrede, *Vlok s.n.*

Table 1.   Continued.

Species	Diploid number 2n	Collection data
G. inandensis Baker	30	S. Africa, Kwazulu-Natal, Inchanga, Goldblatt & Manning 10057
G. longicollis Baker	30	S. Africa, E. Cape, Naudes Nek, Goldblatt & Manning 9542; Mpumalanga, Long Tom Pass, Goldblatt & Manning 9823
G. ochroleucus Baker	30	S. Africa, E. Cape, East London, Batten 1123
G. oppositiflorus Hook.f.	30	S. Africa, E. Cape, near Kei Road, Batten s.n.
G. permeabilis subsp. edulis (Ker Gawl.) Oberm.	28	S. Africa, E. Cape, Rhodes, Batten 1118
G. phoenix Goldblatt & J. C. Manning	30	S. Africa, W. Cape, Bain's Kloof, Goldblatt & Manning 9423
G. pole-evansii Verdoorn	30	S. Africa, Mpumalanga, Denilton, Goldblatt & Manning 9808
G. pretoriensis O. Kuntze	30	S. Africa, Gauteng, Pretoria, Goldblatt & Manning 9799
G. saundersii Hook. f.	30	S. Africa, E. Cape, Naudes Nek, Batten 1114
G. stefaniae Oberm.	30	S. Africa, W. Cape, Montagu, Manning s.n. (NBG)
G. sulcatus Goldblatt	90	Tanzania, Njombe, Lusitu Ridge, Spurrier 804
G. wilsonii (Baker) Goldblatt & J. C. Manning	30	S. Africa, E. Cape, Nahoon, Batten s.n.
G. woodii Baker	30	S. Africa, Mpumalanga, Belfast, Goldbaltt & Manning 9811
Hesperantha baurii Baker	24	Swaziland, near Mbabane, Goldblatt 6609
H. luticola Goldblatt	26 + 1B	S. Africa, N. Cape, Hantamsberg, Goldblatt s.n. (no voucher)
H. radiata (Jacq.) Ker Gawl.	26	Lesotho, Blue Mountain Pass, Schmitz 8531 (ROML)
Ixia brevituba G. J. Lewis	20	S. Africa, W. Cape, Roggeveld, Goldblatt & Manning 8645
I. latifolia var. ramulosa G. J. Lewis	20	S. Africa, N. Cape, Namaqualand, Goldblatt 9241
I. paniculata D. Delaroche	20	S. Africa, W. Cape, Piekenierskloof, Goldblatt 5117
Melasphaerula graminea (L.) N.E. Br.	20	S. Africa, W. Cape, near Soutpan, Goldblatt s.n. (no voucher); near Clanwilliam, Goldblatt 3832
Radinosiphon leptostachya (Baker) N.E. Br.	30	Malawi, Golomoti Mts., Boussard s.n.; Mt. Malosa, Goldblatt 9201
Romulea cameroonensis Baker (= R. campanuloides Baker)	26	Malawi, Zomba Plateau, Goldblatt 9094; Snijman s.n.
R. congoensis Bég.	ca.78	Rwanda, Virunga Mts., D'Arcy 7887
R. c.f. linaresii Parl.	ca.39	Greece, Athens, Goldblatt 5051
Sparaxis caryophyllacea Goldblatt	20	S. Africa, W. Cape, Nardouw Pass, Goldblatt 6162
S. parviflora (G. J. Lewis) Goldblatt	40	S. Africa, W. Cape, without precise locality (no voucher)
S. variegata subsp. metelerkampiae (L. Bolus) Goldblatt	20	S. Africa, W. Cape, Algeria, Goldblatt s.n.
Syringodea bifucata de Vos	12	S. Africa, Gauteng, farm Sandfontein, Davidson 3108
Tritonia chrysantha Fourc.	22	S. Africa, E. Cape, Alicedale, Bayliss 8047
T. florentiae (Phill.) Goldblatt	20	S. Africa, W. Cape, Ceres Karoo, Goldblatt 3912
T. laxifolia Benth.	20	Tanzania, Makambako, Spurrier 601
T. squalida (Aiton) Ker Gawl.	22	S. Africa, W. Cape, S. of Riversdale, Goldblatt 5090
Xenoscapa fistulosa (Klatt) Goldblatt & J. C. Manning	22	S. Africa, N. Cape, Richtersveld, Williamson & Hamer 4428
X. uliginosa Goldblatt & J. C. Manning	22	S. Africa, N. Cape, Namaqualand, Goldblatt 9244

which we consider to be chromosomes. Ancestral base number for the genus is probably $x = 9$, not $x = 10$ as suggested by Kenton and Heywood, making the species counted in South America hexap-

loid. This does not explain the counts of both $2n = 40$ (by Kenton & Heywood) and 84 (by us) in the same Australian species. This species also differs from the South American species of the genus

Table 2. Chromosome numbers in genera of Nivenioideae and Iridoideae. Data are largely from Goldblatt (1971, 1982a) who included reviews of previous reports for the subfamilies, and Kenton & Heywood (1984). Sources other than Goldblatt (1971) are referenced below. Numbers in parentheses after the genera indicate number of species counted out of the total in the genus; parenthetical entries in the base-number column indicate secondary base numbers. Presence of triploids, unless known to be stabilized, and B chromosomes are not included. Genera are arranged alphabetically in subfamilies and tribes according to Goldblatt (1990a) excepting that *Bobartia* has been moved from Iridoideae: Sisyrinchieae to Irideae in light of molecular data (Souza-Chies et al., 1997; M. Chase, pers. comm.).

| Genus | Basic and diploid numbers | | Reference |
	x	$2n$	
Nivenioideae			
Aristea (12/52)	16	32, 64	Goldblatt, 1995
Geosiris (0/1)	uncounted		
Klattia (1/3)	16	32	
Nivenia (4/10)	16	32	
Patersonia (6/20)	?11	22, 42, ca.62	Goldblatt, 1979a
Witsenia (1/1)	16	32	
Iridoideae			
Tribe Sisyrinchieae			
Diplarrhena (2/2)	16	32	Kenton & Heywood, 1984
Libertia (5/8)	19	38, 76, 112	Hair et al., 1967; Kenton & Heywood, 1984
Olsynium (5/11) (incl. *Phaiophleps*)	10(9, 8, ?11)	20, 22, 40, 60, 18, 96	(as *Phaiophleps* and *Sisyrinchium* sects. *Nuno* and *Eriphilema*, e.g. Rudall et al., 1986; Rodriguez, 1986
Orthrosanthus (4/8)	?9(?12, 10)	54, 40, 84, 50	Kenton & Heywood, 1984
Sisyrinchium (40/ca. 80)	9(8, 5, 17)	18, 36, 72, 16, 32, 48, 64, 96, 34	Rudall et al., 1986; Kenton et al., 1987
Solenomelus (1/2)	?8	48	Rudall et al., 1986
Tapeinia (0/1)	uncounted		
Tribe Mariceae			
Neomarica (4/12)	?9(8)	18, 16, 32	Goldblatt, 1982a; Kenton & Heywood 1984
Pseudotrimezia (0/6)	uncounted		
Trimezia (5/20)	?14(13, 10 or 20)	28, 26, 52, 40, 60, 80	Goldblatt, 1982a; Kenton & Heywood 1984
Tribe Tigridieae			
Ainea (0/1)	uncounted		
Alophia (3/5)	14	28	Goldblatt, 1982a; Kenton & Heywood 1984
Calydorea (4/10) (incl. *Catila*)	7	14, 28, 42	Goldblatt, 1982a; Kenton & Heywood 1984
Cardenanthus (0/8)	uncounted		
Cipura (4/8)	7	14, 28[1]	Goldblatt & Henrich, 1987
Cobana (1/1)	14	28	Ravenna, 1974
Cypella (5/20)	7(5)	14, 28, 10	
Eleutherine (2/2)	6	12[1]	Goldblatt & Snow, 1991
Ennealophus (3/5) (incl. *Tucma*)	7	14	Kenton & Heywood, 1984; Martínez & De Azkue, 1987
Fosteria (1/1)	14	28	Molseed, 1970
Gelasine (2/5)	7(6)	14, 12	Kenton & Rudall, 1987
Herbertia (4/8) (= *Trifurcia*)	7	14, 28, 42	Winge, 1959; Kenton & Heywood, 1984
Kelissa (0/1)	uncounted		
Mastigostyla (3/16)	14	28	Huynh, 1965; Martínez & De Azkue, 1987

Table 2. Continued.

| Genus | Basic and diploid numbers | | Reference |
	x	2n	
Nemastylis (3/5)	7	14, 28, 56	Goldblatt, 1982a
Onira (0/1)	uncounted		
Sessilanthera (2/4)	14	28	Cruden, 1972
Tigridia (14/35)	7	14, 28	Molseed, 1970; Kenton & Heywood 1984
Tribe Irideae			
Barnardiella (1/1)	10	20	Goldblatt, 1977
Belamcanda (1/1)	16	32, 64	Nakajima, 1936; Hsu, 1971
Bobartia (8/14)	10	20	Strid, 1972
Dietes (6/6)	10	20, 40, 60	Goldblatt, 1981a
Ferraria (10/10)	10	20, 40, 60	de Vos, 1979
Galaxia (14/15)	9(8, 7, 6)	18, 16, 14, 12	Goldblatt, 1979c, 1984a
Gynandriris (7/9)	6	12, 24	Goldblatt, 1980b
Hermodactylis (1/1)	10	20	Simonet, 1932
Hexaglottis (6/6)	6(7, 5)	12, 14, 10	Goldblatt, 1987
Homeria (34/34)	6(5, 4)	12, 24, 10, 9, 8	Goldblatt, 1980a, 1981b
Iris (185/ca. 225)	? (many diploid numbers occur in this large genus; both polyploidy and dysploidy are frequent)		
Moraea (95/130)	10(9, 8, 7, 6, 5)	20, 40, 18, 16, 12, 24, 48, 10	Goldblatt, 1976, 1986a, 1986b
Pardanthopsis (1/1)	16	32	Simonet, 1932
Roggeveldia (2/2)	6	12, 24	Goldblatt, 1992

[1]Goldblatt & Snow (1991) have shown that the plants associated with the counts of $2n = 12(-14)$ for *Cipura paludosa* and $2n = 14$ for *Eleutherine bulbosa* (Sharma & Talukdar, 1959) were confused with one another. Counts of $2n = 14$ are for *C. paludosa*, while those of $2n = 12(-14)$ are for *E. bulbosa*. The count of $2n = 14$ for the latter reported by Rao (1969) is probably also for *C. paludosa*.
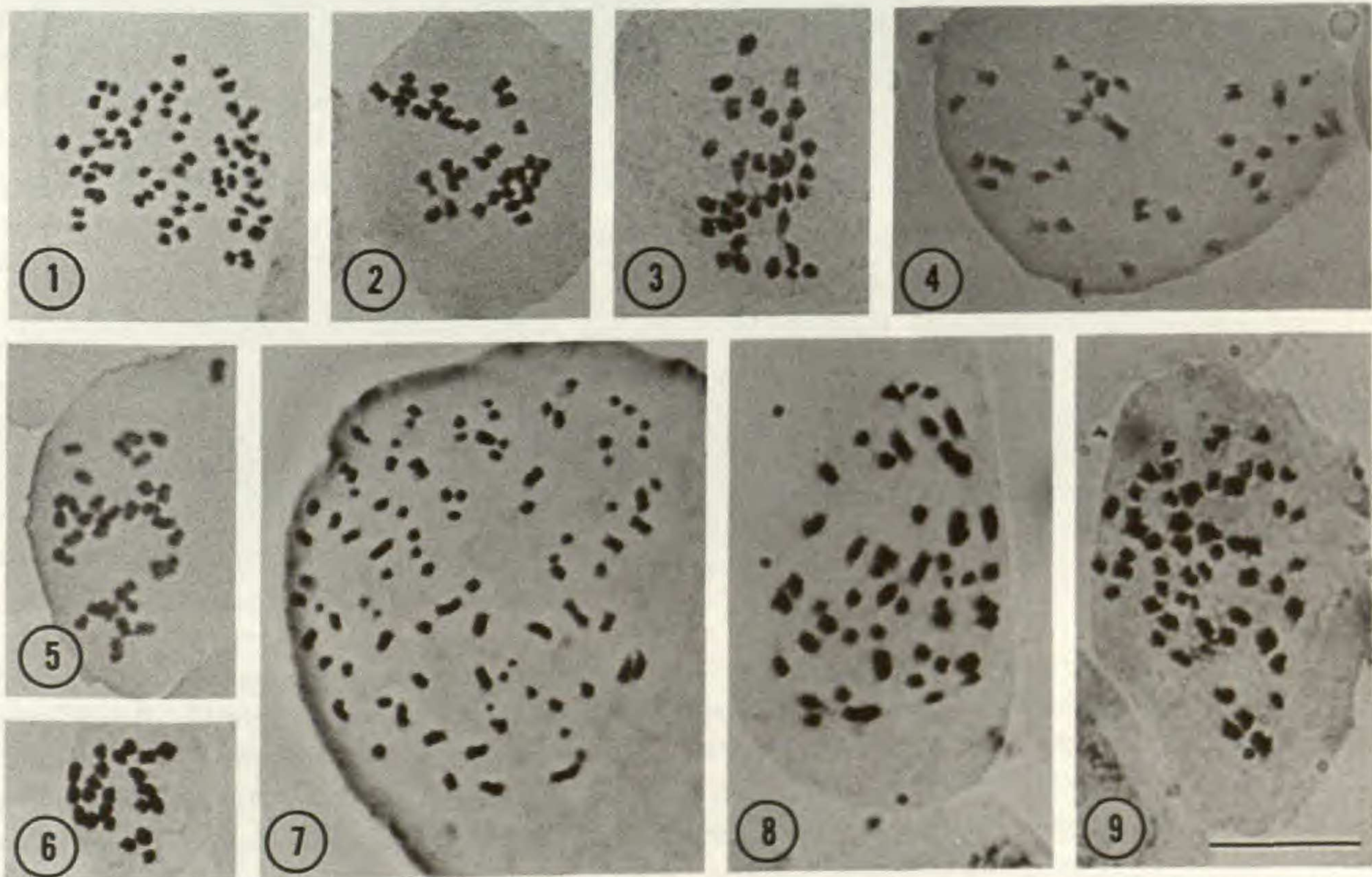
Figures 1–9. Mitotic metaphase in Iridaceae subfamily Nivenioideae (*Aristea* and *Patersonia*) and Iridoideae tribe Sisyrinchieae (*Orthrosanthus*).—1. *Aristea abyssinica* ($2n = 64$).—2. *A. anceps* ($2n = 32$).—3. *A. angolensis* ($2n = 32$).—4. *A. juncifolia* ($2n = 32$).—5. *A. angustifolia* ($2n = 32$).—6. *Patersonia sericea* ($2n = 22$).—7. *Orthrosanthus polystachyus* ($2n = 84$).—8. *O. acorifolius* ($2n = 54$).—9. *O. chimboracensis* ($2n = 54$). Vouchers as given in Table 1. Scale bar, 10 μm.

in having a bimodal karyotype with the larger chromosomes 2–2.3 μm long, and the smaller 0.5–1.2 μm long, a pattern also noted by Kenton and Heywood. More counts are needed in *Orthrosanthus*, for both Australian and South American taxa. Chromosomal characters will likely be relevant to the systematic and phylogenetic understanding of the genus.

We include only one original count in *Sisyrinchium* (Table 1), $2n = 48$, for the annual *S. micranthum*. This agrees with past reports for the species. Ancestral base number for *Sisyrinchium* is most likely $x = 9$. Subgenus *Echthronema* has species based on either $x = 9$, 8, or 17, but most species of subgenus *Sisyrinchium* have $x = 8$ (Kenton & Heywood, 1984) and one annual species has $n = 5$. The related *Olsynium* (including *Sisyrinchium* subg. *Eriphilema*) has base numbers of $x = 10, 9, 8$, and perhaps 11, but the ancestral base number may well be $x = 10$. We conclude that the ancestral base number for Sisyrinchieae may be $x = 10$, based on the pattern so far reported in the tribe (Table 2). The Australian *Diplarrhena*, currently included in Sisyrinchieae, has large chromosomes and $x = 16$. On the basis of chromosome size it accords better with Irideae. Number alone provides no information about its relationships.

Large chromosomes and a base number of $x = 10$ have been postulated to be ancestral for Irideae (Goldblatt, 1990a), and *Bobartia* (usually included in Sisyrinchieae), *Dietes*, and *Ferraria* (Table 2) conform to this pattern. The count here of $2n = 60$ in *D. robinsoniana* (Table 1), the Lord Howe Island endemic and only non-African species of *Dietes*, conflicts with an earlier count of $2n = 20$ in the species (Goldblatt, 1979a). It seems unlikely that *D. robinsoniana* is heteroploid. We question the identity of the plant counted earlier under that name, unfortunately without a voucher. The closely related *D. bicolor* from South Africa is also polyploid, $2n = 40$ (Goldblatt, 1971). The four other species of *Dietes* are diploid, $2n = 20$ (Goldblatt, 1981a).

Our count here of $2n = 40$ for the tropical African *Ferraria glutinosa* confirms a report that the species is tetraploid in Namibia (Goldblatt, 1979b). Interestingly, a diploid population of the species has been reported from Zaire (De Vos, 1979), thus establishing that the species is heteroploid. Of the remaining nine species of *Ferraria*, seven are diploid, *F. divaricata* has diploid and tetraploid subspecies, and two more have both tetraploid and hexaploid populations. *Ferraria* is one of the few African genera of Iridaceae in which polyploidy appears to have played a significant role in its evolution.

Ancestral base number in the large African genus, *Moraea*, is also $x = 10$ (Goldblatt, 1976, 1986a). Our counts for numerous species of the genus with this base number show some degree of variation in their karyotypes (Figs. 11–13). Notably in subgenus *Visciramosa*, *M. elsiae* has a distinctive karyotype in which 5 of the 10 chromosome pairs are telocentric (Fig. 13). The other four species of subgenus *Visciramosa* also have this unusual and presumably derived karyotype (Goldblatt, 1971 and unpublished).

Dysploid reduction in at least four lineages of *Moraea* has resulted in the independent evolution of the secondary base of $x = 6$ (Goldblatt, 1986a). Counts reported here from subgenus *Vieusseuxia*, section *Polyanthes*, and subgenus *Grandiflora* provide examples of the three main groups with $x = 6$ (Figs. 15–18, 21–24). In a fourth lineage, *M. fugax* (subg. *Moraea*) offers a remarkable example of dysploid reduction from $x = 10$ (presumably the ancestral base) to $n = 8, 7, 6$, and 5 within a single polymorphic species (Goldblatt, 1986b). The count here of $2n = 10$ (Fig. 19) is representative of one of several cytotypes in the species.

In subgenus *Vieusseuxia*, karyotypes typically have marked size variation (Figs. 21, 22, 24), the shortest chromosome pair, 7–8 μm long, being about two-thirds to about half as long as the longest pair, 12–14 μm. One of the two longest pairs is always more or less metacentric and the other is acrocentric. A small satellite is consistently present on one of these long pairs. Chromosomes of subgenus *Grandiflora* are consistently larger than elsewhere in the genus and 10–14 μm long. In *Moraea schimperi*, typical of the subgenus (Fig. 23), the chromosomes are acrocentric to nearly telocentric and a small satellite is located on one of the nearly telocentric chromosome pairs. Based on measurement of total chromosome length, we estimate that genome size in *M. schimperi* is some 20–30% larger than in subgenus *Vieusseuxia* or subgenus *Moraea*.

In section *Polyanthes*, e.g., *M. bipartita*, *M. callista*, *M. carsonii*, *M. deserticola* (Figs. 15–18), chromosome size variation is modest. The chromosomes are 7–12 μm long and all are more or less acrocentric. This pattern resembles closely that of the karyotypes of the southern African genera, *Hexaglottis*, *Homeria*, and *Roggeveldia* (Goldblatt, 1980a, 1987). The karyotypic similarity among these three taxa suggests common ancestry with *Moraea* sect. *Polyanthes*. This possibility should be considered in future studies of the phylogeny of Irideae. We have noted an unusual condition in *M.*
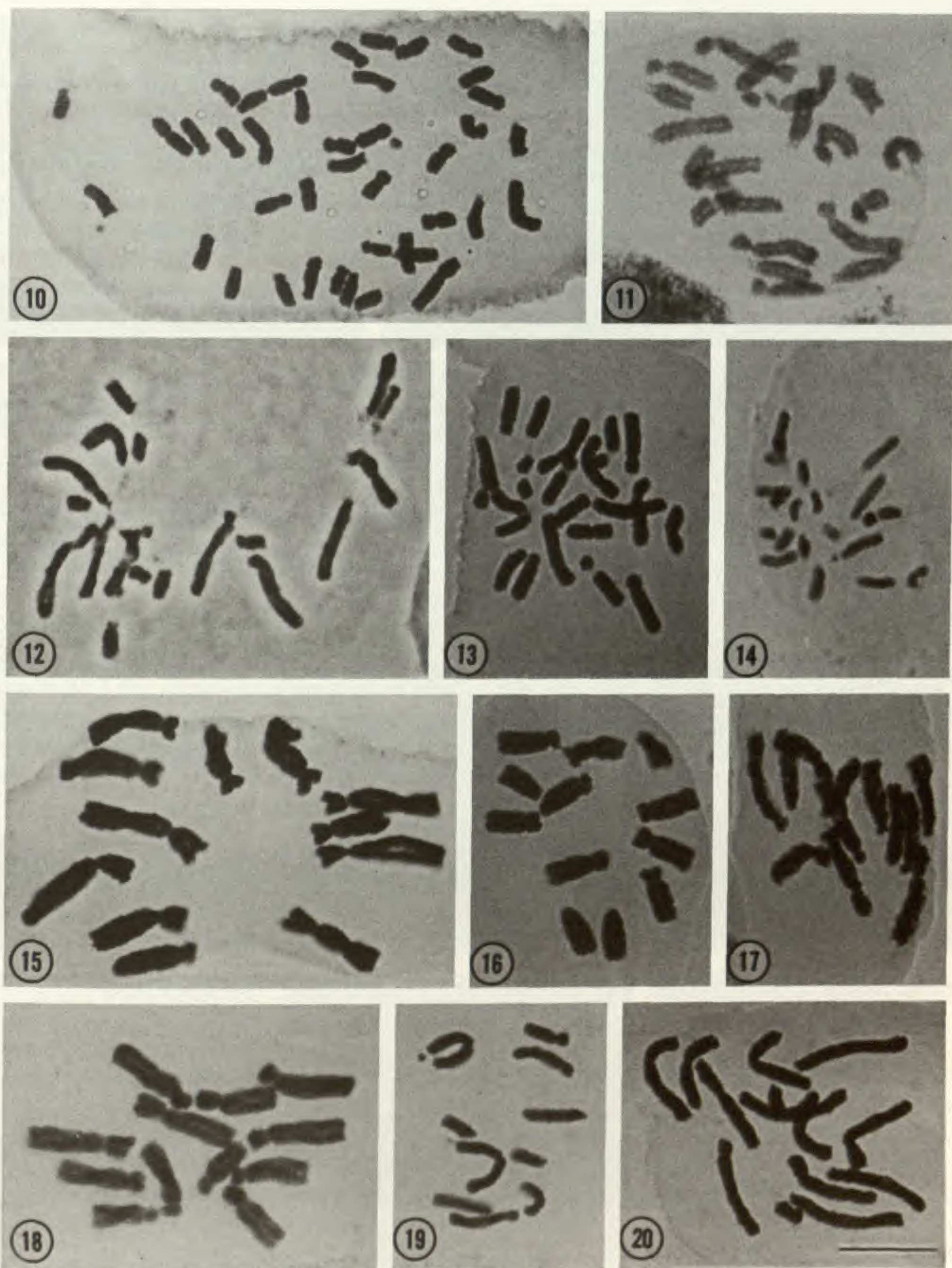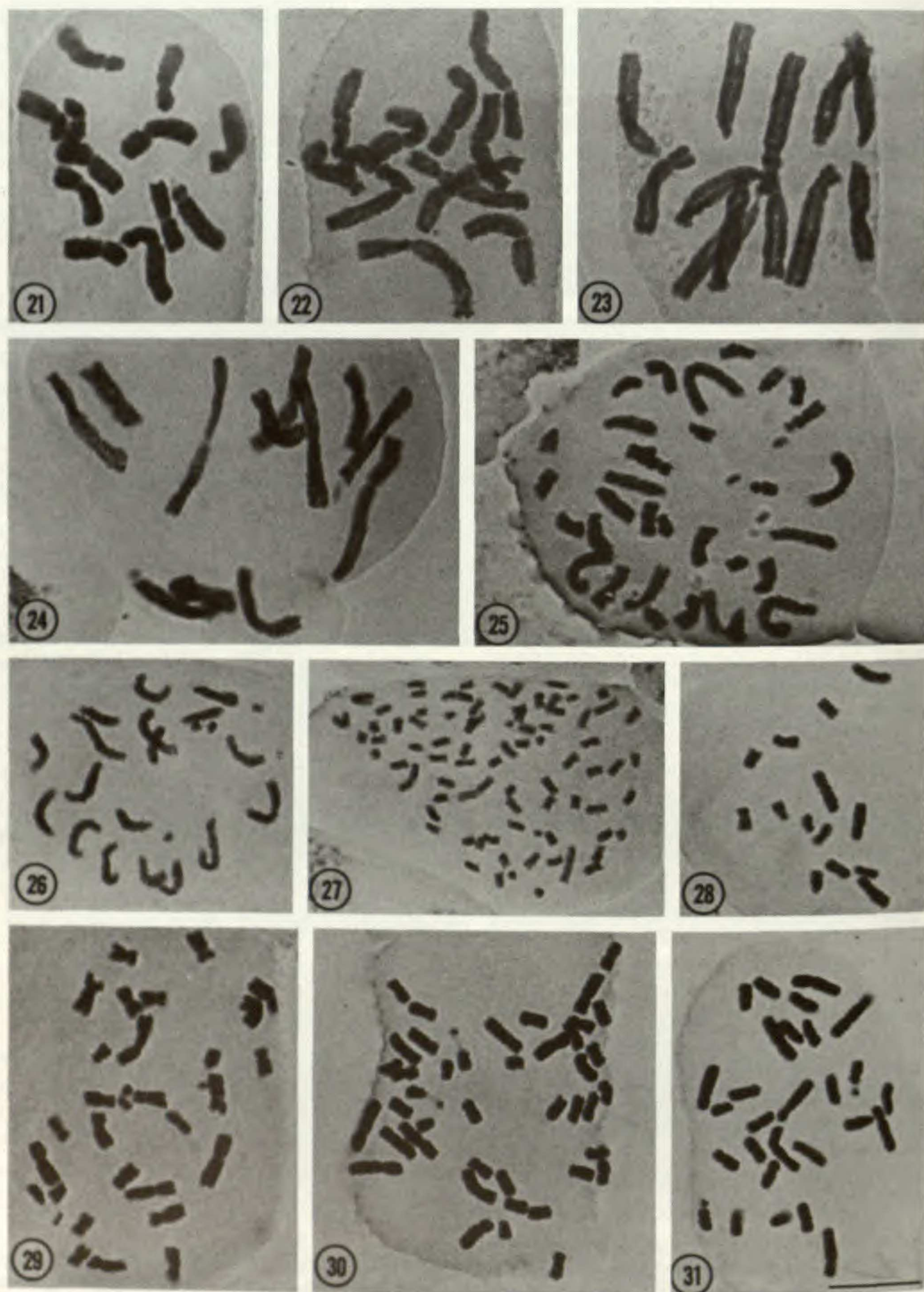
Figures 10–20.   Mitotic metaphase in Iridaceae subfamily Iridoideae tribe Irideae.—10. *Iris tridentata* (2*n* = 40).—11. *Moraea anomala* (2*n* = 20).—12. *M. namibensis* (2*n* = 20).—13. *M. elsiae* (2*n* = 20).—14. *Barnardiella spiralis* (2*n* = 20).—15. *Moraea carsonii* (2*n* = 12).—16. *M. deserticola* (2*n* = 12).—17. *M. bipartita* (2*n* = 12).—18. *M. callista* (2*n* = 12).—19. *M. fugax* (2*n* = 10).—20. *M. fergusoniae* (2*n* = 12). Vouchers as given in Table 1. Scale bar, 10 µm.

callista. One population examined has a karyotype consisting of matching pairs (Fig. 46A), but another is karyotypically heterozygous (Fig. 46B) and has one long metacentric chromosome and one very short metacentric. Further studies in this tropical African species are needed to elucidate the significance of this situation.

Unusual in Iridaceae, the only three species of *Homeria* that exhibit dysploidy, *H. pallida, n* = 6 and 4, and *H. tenuis* and *H. flavescens*, 2*n* = 10,

Figures 21–31. Mitotic metaphase in Iridaceae subfamily Iridoideae tribes Irideae (*Moraea*), Mariceae (*Neomarica* and *Trimezia*), and Tigridieae (*Cypella*, *Calydorea*, and *Herbertia*).—21. *Moraea incurva* (2n = 12).—22. *M. tulbaghensis* (2n = 12).—23. *M. schimperi* (2n = 12).—24. *M. unguiculata* (2n = 12).—25. *Neomarica caerulea* (2n = 32).—26. *N. cf. northiana* (2n = 18).—27. *Trimezia martinicensis* (2n = 80).—28. *Cypella herbertii* subsp. *wolfheugelii* (2n = 14).—29. *Calydorea pallens* (2n = 28).—30. *Herbertia lahue* (2n = 42).—31. *H. pulchella* (2n = 28). Vouchers as given in Table 1. Scale bar, 10 μm.

9, and 8, are complex heterozygotes (Goldblatt, 1980c). The complex heterozygosity in these species is associated with dysploidy, itself evidently achieved by unequal reciprocal translocation. In *Hexaglottis*, the specialized *H. virgata* has populations with $n = 6, 5$, or 7, the latter number evidently consistent for subspecies *karooica*. In the latter there is an additional pair of very small chromosomes that resemble B chromosomes except that their number is stable. In populations of subspecies *virgata* with $n = 5$, the karyotype has an extra pair of metacentric chromosomes and the numerical change is presumed to have been accomplished by conventional Robertsonian fusion (Jones, 1974, 1977; Goldblatt, 1987).

Our counts for four populations of *Moraea fergusoniae* are $2n = 12$. The previous count of $2n = 20$ for the species (Goldblatt, 1971) is clearly incorrect. The karyotype (Fig. 20) is notable in having the two longest chromosomes acrocentric, ca. 14 μm long, and bearing very large satellites that exceed the short arms of the chromosomes. The unusual karyotype does not help assess the affinities of the species, the subgeneric disposition of which is uncertain. In its small, long-lasting flower with trilobed inner tepals it corresponds with subgenus *Vieusseuxia*, but the presence of several leaves in the species is inconsistent with that subgenus, all species of which have a single foliage leaf.

The southern African and Mediterranean *Gynandriris* also has $x = 6$ (Goldblatt, 1980b). Two species of the genus have a karyotype that accords fairly well with *Moraea* sect. *Polyanthes*, but most species have a second karyotype in which the longest pair is metacentric, a pattern reminiscent of *Moraea* subg. *Vieusseuxia*. The monotypic *Barnardiella* has $x = 10$ and a karyotype like that in many species of *Moraea* subg. *Moraea* (e.g., Figs. 11–13), also $x = 10$. In *Barnardiella* the longest chromosomes are ca. 5.6 μm and shortest ca. 2 μm (Fig. 14). Presence of blue flowers and an included ovary in *Barnardiella* point to a relationship close to species such as *M. tortilis* and *M. rigidifolia*, which have these same morphological features.

Galaxia appears to be a dysploid genus with an ancestral base of $x = 9$. The basic karyotype (Goldblatt, 1979c) broadly resembles that of the ancestral karyotype in *Moraea* except for the difference in base number and generally somewhat smaller chromosomes. The six species of subgenus *Eurystigma* display a dysploid series with different species having $x = 9, 8, 7$, and 6. This has been interpreted as a descending dysploid sequence based on the morphology of the species concerned (Goldblatt, 1979c, 1984a).

The Northern Hemisphere *Iris*, one of the two largest genera of Iridaceae, is cytologically complex, and ancestral base number is uncertain. The base number $x = 20$ is frequent in the less specialized subgenus *Limniris*, but subgenus *Iris* almost certainly has $x = 12$ (excluding polyploidy, the most common numbers are $n = 12, 11, 10$, and 9). Based on an analysis of the many counts available in the literature, subgenus *Reticulata* (sometimes treated as a genus, *Iridodictyum*) has $x = 10$ ($n = 10, 9, 8$); subgenus *Xiphium* may have $x = 18$ ($n = 18, 17, 16, 14$); and subgenus *Scorpiris* (syn. *Juno*) appears to have $x = 12$ ($n = 12, 11, 10, 9$, and even 13 and 15).

The single count included here for *Iris* was made because *I. tridentata* (subg. *Limniris*), the only North American species uncounted, was available to us. The count of $2n = 40$ and large chromosomes 3.3–6.3 μm long (Fig. 10) are consistent with several species of section *Limniris*, common numbers for which are $2n = 44$ and 40. However, our count differs from the available reports for both *I. setosa* ($2n = 38, 36$, and 54) and *I. hookeri* ($2n = 38$), the only other species of series *Tripetalae* and presumably the closest relatives of *I. tridentata* (Mathew, 1981). In their comparatively large size, the chromosomes of *Iris* species agree well with other genera of Irideae.

Basic chromosome number in Mariceae (syn. Trimezieae), one of two exclusively New World tribes of Iridoideae (Goldblatt, 1990a), is uncertain (Table 2). Of the three genera currently recognized, *Pseudotrimezia* is uncounted and the pattern in the remaining two is confused. The five species of *Trimezia* counted (Fig. 27) have diploid numbers of $2n = 26, 28, 40, 52, 54, 60$, and 80 (Table 2), numbers that seem to have little relationship to one another. There is also a remarkable variation in chromosome size among the species counted (Kenton & Heywood, 1984). The two species with numbers based on 10, *T. martinicensis* ($2n = 40, 80$) and *T. sincorana* ($2n = 60$), also have the smallest chromosomes. They are closely related and appear to be derived on the basis of their specialized floral morphology ($2n = 54$ reported by Kenton & Heywood (1984) for *T. martinicensis*, is almost certainly based on another species). *Trimezia martinicensis* is known to be autogamous, also a derived condition. Hence, the base of $x = 10$ is probably also derived in these species. The less specialized *T. steyermarkii* has $n = 26$ and *T. martii* has $n = 14$, and the vegetatively specialized *T. fosteriana* has $n = 13$. More counts are needed in *Trimezia* before it will be possible to make sense of the pattern here. Tentatively, we suggest that $x = 14$ may be the ances-
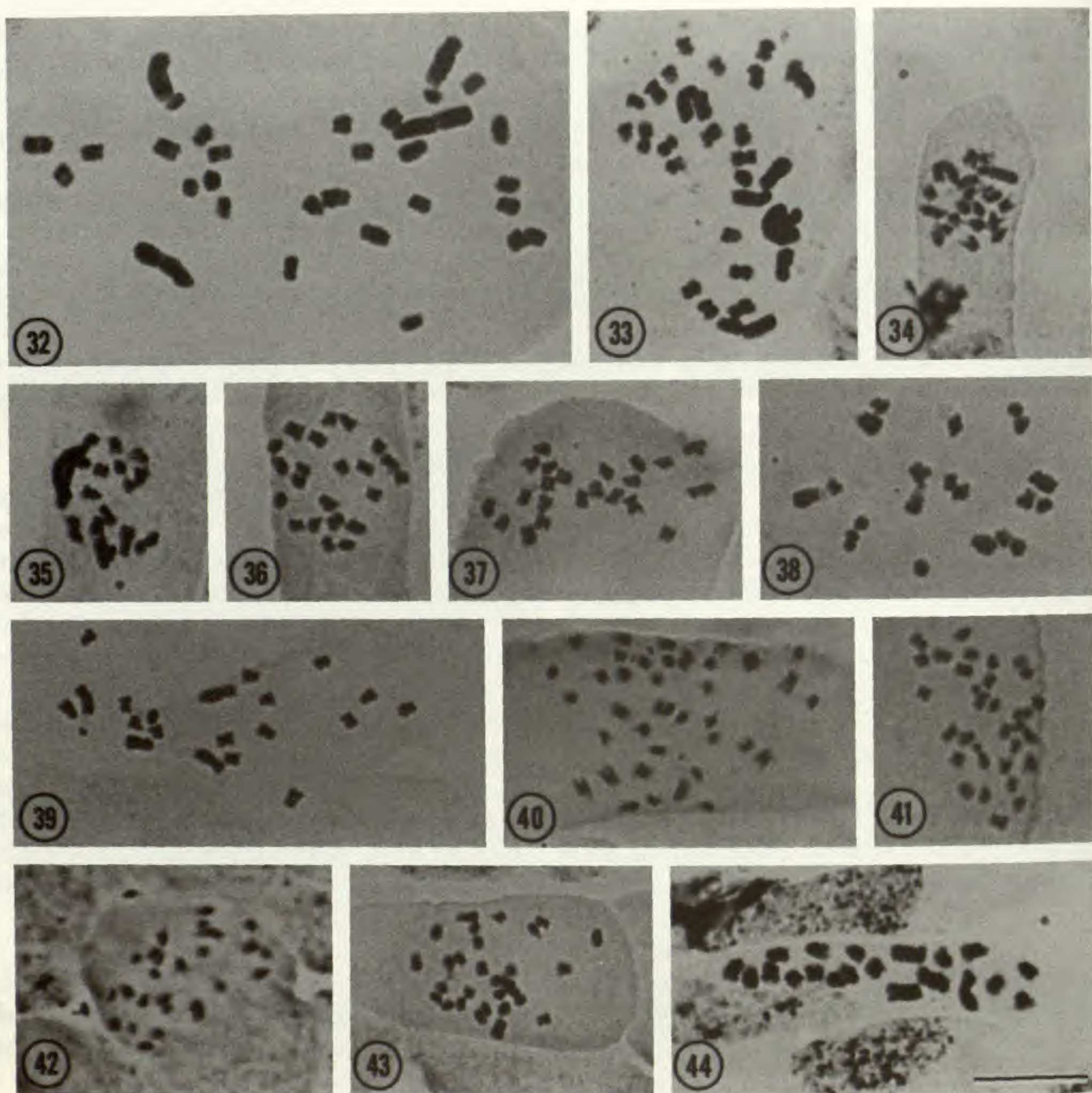
Figures 32–44. Mitotic metaphase in Iridaceae subfamily Iridoideae tribe Tigridieae and subfamily Ixioideae.—32. *Alophia drummondii* (2n = 28).—33. *Cobana guatemalensis* (2n = 28).—34. *Micranthus juncifolius* (2n = 20).—35. *Lapeirousia barklyi* (2n = 16).—36. *Xenoscapa fistulosa* (2n = 22).—37. *X. uliginosa* (2n = 20).—38. *Dierama inyangensis* (2n = 20).—39. *Ixia latifolia* (2n = 20).—40. *Sparaxis parvifolia* (2n = 40).—41. *Radinosiphon leptostachya* (2n = 30).—42. *Romulea cameroonensis* (2n = 26).—43. *Gladiolus ochroleucus* (2n = 30).—44. *Tritonia laxifolia* (2n = 20). Vouchers as given in Table 1. Scale bar, 10 μm.

tral base for the genus. Cycles of polyploidy and dysploid reduction then would best explain the remaining base numbers.

The related *Neomarica*, included in *Trimezia* by Ravenna (1976), is specialized in having a winged aerial stem and branches crowded apically. *Neomarica northiana* has 2n = 18 (Fig. 26), a count confirmed here, as does *N.* cf. *vittata* (Kenton & Heywood, 1984). Reports for *N. gracilis* include 2n = 18, 40, and 32. Some of these counts are almost certainly from misidentified plants. The Central American *N. variegata* (often confused with *N. gracilis* in the literature), specialized in its red, fleshy seeds, has 2n = 16 and *N. caerulea* has 2n = 32 (Fig. 25). The ancestral base number for the

genus is most likely x = 9, and x = 8 is evidently derived by dysploid reduction. The variation already evident in both *Trimezia* and *Neomarica* makes it essential that chromosome cytology be included in future systematic and phylogenetic studies of these genera.

Unlike Mariceae, the pattern in the other exclusively American tribe Tigridieae is reasonably clear (Figs. 28–31). The ancestral base number appears to be x = 7, and this is the only base number in most genera of subtribe Cipurinae counted, and the only base in the other subtribe, Tigridiinae (Table 2). The base of x = 7 is strongly conserved despite a fair degree of karyotypic diversity. Bimodality is common and is also conserved despite variation in
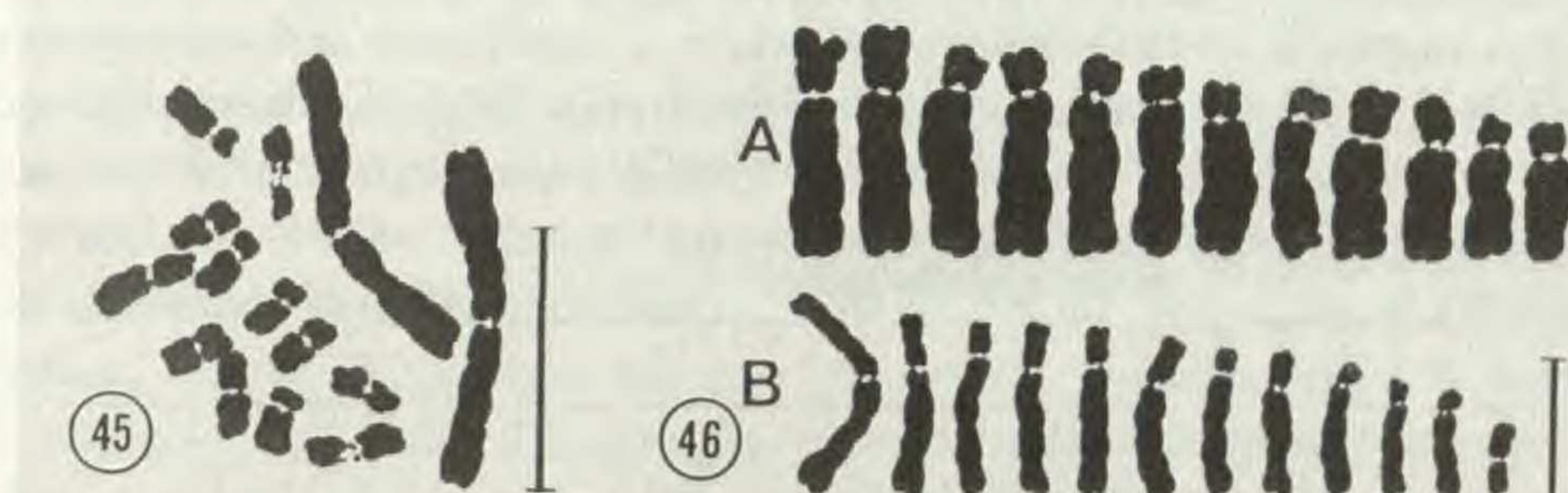
—Figure 45.   Mitotic metaphase in *Ennealophus foliosus* (2n = 14) (Iridoideae–Tigridieae).—Figure 46. Metaphase chromosomes of *Moraea callista* (2n = 12) (Iridoideae–Irideae). A: population from Lusitu Ridge with normal chromosome complement; B: population from the Kitulo Plateau showing structural heterozygosity. Vouchers as given in Table 1. Scale bar, 5 μm.

chromosome and karyotype size (Kenton et al., 1990). Among seven species of *Cypella* and *Hesperoxiphion* (a genus sometimes included in *Cypella*), all with *x* = 7, chromosome size varies considerably. A more than three-fold difference in total DNA among the species has been demonstrated by Kenton et al. (1990). Yet bimodality and relative sizes of the chromosomes within the karyotypes of each species are maintained.

A particularly distinctive karyotype is present in *Ennealophus* (including *Tucma*) (Fig. 45). All three species counted (of a total of five) have one long metacentric pair, ca. 7 μm long, and six much shorter pairs, ca. 1.5 μm long, one of which has a satellite larger than the short chromosome to which it is attached (see also Kenton & Heywood, 1984).

Cypella plumbea, sometimes segregated as *Phalocallis* (Ravenna, 1977), has 2n = 10 and is exceptional here (counts for the few other species that have been placed in *Phalocallis* would be interesting). The two species of *Eleutherine*, an apparently very derived genus, have *x* = 6 (Goldblatt & Snow, 1991) as does *Gelasine intermedia* (= *G. azurea*). The latter is an autogamous, complex heterozygote (Kenton & Rudall, 1987) with an apparently derived floral morphology. The only other species of *Gelasine* counted has 2n = 14 (Ravenna, 1984).

Polyploidy is common in Tigridineae, and a few genera are exclusively polyploid. In *Tigridia* most species so far counted (e.g., Figs. 32, 33) have *x* = 14 (Table 2), including all those from Central America and Mexico (Molseed, 1970; Kenton & Heywood, 1984), but at least two South American species have *n* = 7. The only counts in *Alophia* (the species of which are sometimes confused nomenclaturally with those of *Herbertia*), *Fosteria*, *Cobana*, and *Sessilanthera* are 2n = 28. At least the three latter, all small genera closely related to Central American *Tigridia*, and probably nested within it, may be exclusively tetraploid. Despite

their polyploidy, karyotypes in *Cobana*, *Alophia*, *Tigridia*, and their allies consistently have one long metacentric chromosome pair and one submetacentric pair. In *Cobana* (Fig. 33) it is possible to tell by careful observation that the long and apparently submetacentric chromosome pair is actually acrocentric with a long satellite attached to the short chromosome arm. The mismatch of the four long chromosomes suggests early chromosomal rearrangement in a polyploid ancestor of the group or a hybrid origin from parents with different karyotypes.

3. IXIOIDEAE

Small chromosomes, usually 1–2.5 μm long (Figs. 34–44), are plesiomorphic in this, the largest subfamily, and are found in most genera (Goldblatt, 1971). Ixioideae are otherwise defined by several morphological and palynological features (Goldblatt, 1990a; Goldblatt et al., 1991). By fusion one or more larger chromosome pairs have evolved in some genera, notably *Lapeirousia* (Goldblatt & Takei, 1993) and *Crocus* (Brighton, 1976; Brighton et al., 1983). In *Lapeirousia* the two long chromosomes present in all species are 4.1–6.5 μm long, and in most species the remaining 12–18 chromosomes are 1–2 μm long, thus typical of Ixioideae. Basic numbers are generally high in the subfamily (Table 3). Dysploidy and the development of secondary base numbers, known in a few genera, are discussed below.

Freesia, including the species of *Anomatheca* transferred here (Goldblatt & Manning, 1995), and *Xenoscapa* (Figs. 36, 37) have *x* = 11 and all species counted are diploid, 2n = 22 (Table 3). Similar karyotypes with *x* = 11 characterize most species of *Tritonia* and *Crocosmia*, genera that are closely allied to one another and probably closely related to *Freesia* (Goldblatt, 1971,

Table 3. Chromosome numbers in genera of Ixioideae. Data largely from Goldblatt (1971), who included references to earlier studies. Other sources are referenced below. Numbers in parentheses after the genera indicate number of species counted out of the total in the genus; parenthetical numbers in the base number column indicate secondary base numbers. Presence of triploids, unless known to be stabilized, and B chromosomes are not included in the table.

Genus	Basic and diploid numbers		Reference
	x	$2n$	
Tribe Pillansieae			
Pillansia (1/1)	10	40	Goldblatt & Takei, 1993
Tribe Watsonieae			
Lapeirousia (32/40)	10(9, 8, 6, 5, 4, 3)	20, 18, 16, 12, 10, 8, 6	Goldblatt, 1990b; Goldblatt & Takei, 1993
Micranthus (3/3)	10	20	
Savannosiphon (1/1)	8	16	Goldblatt & Marais, 1979
Thereianthus (3/7)	10	20	
Watsonia (31/52)	9	18	Goldblatt, 1989a
Tribe Ixieae			
Babiana (20/64) (incl. Antholyza)	7	14	
Chasmanthe (2/3)	10	20	
Crocosmia (6/9)	11	22	de Vos, 1984
Crocus (79/ca.80)	?6 (uncertain: many base numbers recorded including much polyploidy, sometimes within a species, Mathew, 1982)		
Devia (1/1)	10	20	Goldblatt & Manning, 1990
Dierama (7/44)	10	20	
Duthieastrum (1/1)	10	20	de Vos, 1974b (as Duthiella)
Freesia (13/15) (incl. Anomatheca)	11	22	Goldblatt, 1972 (as Anomatheca), 1982b
Geissorhiza (43/82)	13	26, 39, 52	Goldblatt, 1985
Gladiolus (85/255) (incl. Homoglossum)	15(14, 13, 12, 11)	30, 60, 90, 120, 28, 26, 24, 22	Goldblatt et al., 1993
Hesperantha (32/ca. 65) (incl. Schizostylis)	13(12)	26, ca.50, ca.72–76	Goldblatt 1984b
Ixia (14/45)	10	20, 40	
Melasphaerula (1/1)	10	20	(not x = 11, Goldblatt, 1971)
Radinosiphon (1/1)	15	30	
Romulea (ca.80/ca. 90)	13 or 12(14, 11, 10, 9)	26, 28, 24, 22, 20, 18, 30, 52, 78	de Vos, 1972
Sparaxis (10/13) (incl. Synnotia)	10	20, 40	
Syringodea (7/8)	6(11)	12, 22	de Vos, 1974a
Tritonia (15/28)	11(10)	22, 20, 44	de Vos, 1982
Tritoniopsis (6/22) (incl. Anapalina)	?16(15)	32, 30	Goldblatt, 1990c
Xenoscapa (2/2)	11	22	Goldblatt, 1972 (as Anomatheca)
Zygotritonia (1/4)	7	14	Goldblatt, 1989b

1991; Shneyer, 1990; Rudall & Goldblatt, 1991). Counts here for *T. florentiae* and *T. laxifolia* (Fig. 44), $2n = 20$, are the first records for both species and the only counts in the genus not based on $x = 11$. We assume that these are examples of dysploid reduction by fusion. *Tritonia florentiae* is specialized in *Tritonia* in being acaules-

cent, or almost so, and it does not seem closely related to *T. laxifolia*, indicating independent dysploid reduction twice in the genus. *Chasmanthe* and *Devia*, evidently closely related to *Tritonia* and *Crocosmia* (de Vos, 1984; Goldblatt & Manning, 1990), have $x = 10$, additional examples of dysploid reduction in this alliance. *Du-*

thieastrum, which may be another specialized derivative of this group, also has $x = 10$.

Counts here for *Dierama*, *Ixia*, and *Sparaxis*, all $x = 10$, are consistent with several other reports for these genera (Goldblatt, 1971). There is, however, an important difference between their karyotypes. In *Dierama* and *Ixia* the karyotypes are bimodal, with two relatively long pairs 2.3–2.6 μm long, and eight shorter pairs 1–1.7 μm long (Figs. 38–39), but in *Sparaxis* (Fig. 44) the chromosomes are all small, 0.9–1.6 μm long (Fig. 40). In two of the species of *Ixia* in which we could distinguish satellites, *I. polystachya* and *I. latifolia*, they were attached to the long arms of long chromosomes (Fig. 39). How consistent this is in *Ixia* is uncertain, but in *I. acaulis* (Goldblatt & Manning, 1993) the satellites (not illustrated there) are in the normal position on the distal end of the short arms of two long chromosomes. In *Dierama* and *Sparaxis* the satellites are in the conventional position on the short arm of a long chromosome pair. Earlier reports of the satellites on short chromosome arms in *Ixia* (Goldblatt, 1971) should be confirmed using more refined techniques.

The difference between the karyotypes of *Sparaxis* (now including *Synnotia*) and *Dierama* and *Ixia*, the two genera with which it has often been closely associated (Lewis, 1954, Goldblatt, 1969), suggests that the affinities of *Sparaxis* may lie elsewhere, or at least are not close to the aforementioned genera. Fundamental differences in their leaf margin anatomy (Rudall & Goldblatt, 1991) support this contention. The count here for *S. parviflora* (Goldblatt, 1991) is the first record of polyploidy in the genus (but this should be confirmed for additional populations).

Our counts for two populations of the monotypic African genus, *Radinosiphon*, $2n = 30$ (Fig. 41), confirm past reports for this genus (Table 3), apparently related to *Gladiolus*, which has the same ancestral base number and similar karyotype (Goldblatt et al., 1993). Total chromosome length in *Radinosiphon* is some 10–15% less than in several species of *Gladiolus* that we have examined, but the significance of this in connection with their possible close relationship cannot yet be assessed. Counts here for *Gladiolus*, $2n = 30$ for 12 species, $2n = 28$ for *G. permeabilis* subsp. *edulis*, and $2n = 90$ for the tropical African *G. sulcatus*, include the first reports for nine species. The karyotypes are consistent with the majority of counts for the genus. The count of $2n = 28$ for *G. permeabilis* does not accord with previous counts for the species. Most likely the population we examined is dysploid

and not representative of the entire species or even subspecies.

In the monotypic, western southern African *Melasphaerula* we found $2n = 20$ in two separate populations (Table 1). We suspect that the only other count for the genus, $2n = 22$ (Goldblatt, 1971), is incorrect. *Melasphaerula* is believed to be most closely related to *Geissorhiza* and *Hesperantha*, with which it shares woody corm tunics. The two latter genera have an ancestral base number of $x = 13$ (Goldblatt, 1971, 1984b), a marked difference from the base number in *Melasphaerula*. Additional counts here (Table 3) for *Geissorhiza* and *Hesperantha* confirm $x = 13$ and the predominance of diploidy, $2n = 26$, in both genera. Our count for the eastern southern African *H. baurii*, $2n = 24$, establishes a new, and evidently, secondary base number in *Hesperantha*. More counts for this widespread and common southern African species and its close relatives are needed before the significance of our report of dysploidy can be gauged.

Our observations here for *Romulea cameroonensis* (Fig. 42) and *R. congoensis* are consistent with the small chromosome size (ca. 0.9–2.2 μm) and range of base numbers reported for the genus (de Vos, 1972). However, our count of $2n = 26$ in *R. cameroonensis* (Fig. 42), based on plants from tropical Africa, differs from de Vos's report of $2n = 22$ for the species (as *R. campanuloides*) in southern Africa. The possibility that tropical and southern African plants assigned here are different species should be considered. *Romulea congoensis*, $2n =$ ca. 78 and not before counted, appears to be hexaploid on a base of $x = 13$. The population of *R. linaresii* from Greece with $2n =$ ca. 39 studied here may be triploid (on a base of $x = 13$) or alternatively tetraploid on a base of $x = 10$. Particularly small chromosomes in the species make accurate counting difficult.

The ancestral base number for *Romulea* was suggested by de Vos (1972) to be $x = 12$, but $x = 13$, which seems to be an equally likely ancestral base, is common. Lower base numbers in *Romulea*, $x = 11$, 10, and 9, seem almost certainly to be derived and occur in specialized lineages. The question of ancestral base number in the genus should be reexamined in the light of phylogeny, at present poorly understood. If *Romulea* is related to *Geissorhiza* and *Hesperantha* as suggested by Goldblatt (1991) then an ancestral base number of $x = 13$ seems likely for the genus on the basis of outgroup comparison.

The single count reported here for *Crocus* (Table 1), $2n = 28$ in *C. longiflorus*, confirms past records for that species, as does the count for *Syringodea*

bifucata (= *S. bicolor*), $2n = 12$. The latter count is for plants from Gauteng Province, South Africa, where the genus was not recorded until 1983 (de Vos, 1983). Basic number in *Syringodea* is most likely $x = 6$.

The ancestral base number for Ixioideae is most likely $x = 10$, evidently the base number for tribes Pillansieae and Watsonieae (Table 3). The ancestral base number in Ixieae may also be $x = 10$, but genera less specialized as regards leaf anatomy and seed characters (Goldblatt & Manning, 1995) have higher base numbers, and it is equally likely that $x = 10$, present in a few genera of the tribe, is secondary. At least *Geissorhiza*, *Gladiolus*, *Hesperantha*, *Radinosiphon*, *Romulea*, and *Tritoniopsis*, all with ancestral base numbers between $x = 16$ and 13 (Table 3), are paleopolyploid. We suspect that *Syringodea* ($x = 6$) is a dysploid derivative of an ancestor shared with *Romulea*. Both have inflorescences reduced to solitary flowers and similar asymmetric corms with woody tunics. The single species of *Syringodea* with $x = 11$ (Goldblatt, 1971; de Vos, 1976) is almost certainly a secondary hypotetraploid. Notably low base numbers characterize *Babiana* and *Zygotritonia* (Table 3); although both have $x = 7$, they are probably not closely related (Goldblatt, 1989b).

Extensive dysploid series in Ixioideae are restricted to just 4 genera, *Lapeirousia*, *Gladiolus*, *Romulea*, and *Crocus*, out of a total of 28. Limited intrageneric dysploidy occurs in *Syringodea*, as noted above, and is reported here for the first time in two species of *Tritonia* and one of *Hesperantha*. Thus, the pattern outlined by Goldblatt (1971) for Ixioideae of genera each having a single base number must be modified. Although most genera do have a single base number and exhibit little or no polyploidy, significant dysploidy has been discovered in *Gladiolus* since that review (Goldblatt et al., 1993). Most species of the genus have $x = 15$, but among the small-flowered tropical African species numbers include $n = 14, 13, 12,$ and 11. The pattern of dysploidy in *Lapeirousia* has also been found to be more extensive than previously thought (Goldblatt, 1990b). As hypothesized by Goldblatt and Takei (1993) there is a striking example of dysploid reduction from $x = 10$ to 4 followed by polyploid increase and further reduction from $n = 6$ to $x = 3$ in *Lapeirousia* subg. *Paniculata*. *Gladiolus* and *Lapeirousia* must, therefore, be added to the list of genera of Ixioideae that have extensive dysploid sequences.

Dysploid trends appear consistently to be descending sequences. In *Tritonia florentiae* and *Syringodea unifolia* the species are evidently derived

in their respective genera, the first specialized in its acaulescent habit and the second in having a solitary and terete leaf. In *Gladiolus* all the dysploid species appear more specialized than those with the presumably ancestral $x = 15$ (Goldblatt et al., 1993). Moreover, they appear to belong to at least three, and probably four, separate lineages. Likewise, in *Romulea* members of primitive sections have $x = 12$ or 13, and those of derived sections have $x = 11, 10,$ or 9 (de Vos, 1972).

Cytological patterns in *Crocus*, last of the genera of Ixioideae with extensive dysploidy, are complex (Mathew, 1982) and remain to be satisfactorily explained. Both dysploidy and polyploidy have been significant in the cytological evolution of the genus. Provisionally we suggest an ancestral base of $x = 6$ for the genus, a hypothesis based on outgroup comparison (the immediately related *Syringodea* has $x = 6$) and on the pattern of counts in section *Crocus* (summarized by Mathew, 1982), which includes the more primitive members of the genus. From this base we assume dysploid reduction to $x = 4$, perhaps in several lines, and repeated polyploidization on bases of 6, 5, 4, and 3.

REVIEW OF GENOME SIZE

Genome sizes have been established for a number of Iridaceae and, as in many other families, have been found to vary considerably, even within genera. In Iridoideae, species of *Sisyrinchium* (Kenton et al., 1987) have basic genome sizes (adjusted for polyploidy), i.e., 1C values, of 0.48–0.73 pg in subgenus *Sisyrinchium* (= sect. *Bermudiana*) and 0.25–2.10 pg in subgenus *Echthronema*. The related *Olsynium* (= *Phaiophleps* plus *Sisyrinchium* sections *Filifolium* and *Nuno*) typically has larger genomes among the temperate southern South American species with 2.66–3.26 pg, but the octoploid North American member of the genus, *O. douglasii*, has a basic genome size of 0.49 pg.

Among Tigridieae, which typically have larger chromosomes than *Sisyrinchium*, 1C genome sizes range from 2.03–2.39 pg in *Cypella* and 1.24–1.34 pg in three species of *Hesperoxiphion* (Kenton et al., 1990), but *H. huilense* has a genome size of 4.38 pg, despite also being diploid. These genome sizes were determined cytophotometrically against a standard, *Hordeum vulgare*, genome size of which is 11.12 pg (2C) or 5.56 pg (1C), a value recently confirmed by Arumuganathan and Earle (1991). Comparable genome sizes of 1.47–2.48 have also been reported by Martínez and De Azkue (1987) for five species of *Eleutherine*, *Ennealophus*, and

Mastigostyla, but *Calydorea* sp. has a smaller genome of 0.98 pg.

Among Old World Iridoideae, Irideae have comparatively larger genomes than Tigridieae, although genome sizes vary considerably among diploid members of the tribe (Goldblatt et al., 1984). Genome sizes reported by Goldblatt et al. (1984) using *Zea mays* as a standard need correcting. Genome size in maize has now been found to be C = 4.75–5.63 pg (Arumuganathan & Earle, 1991; Bennett & Smith, 1991), somewhat lower than the estimate of 6.3 pg used by Goldblatt et al. The 4C values published by Goldblatt et al. (1984) thus require adjustment by a factor of 0.75–0.84. We make a correction of 0.75 here in the figures given below (the strain used in the Goldblatt et al. study had a karyotype without knobs or structural additions). Basic 1C genome sizes (corrected for polyploidy) in Irideae are 1.20 pg in *Galaxia* to 12.24 pg in *Iris histrio*.

Moraea, the only genus investigated extensively, has larger basic genomes in subgenus *Vieusseuxia*, 4.93–6.81 pg ($x = 6$) than in subgenus *Moraea*, 3.74–4.32 ($x = 10$). In *Homeria* (including *Sessilistigma*) and *Hexaglottis* (both $x = 6$) 1C genomes range from 3.87 to 5.94 pg in the five species examined. The larger genomes evident in *Moraea* subg. *Grandiflora* (discussed above) have not yet been measured for total DNA. One species of *Iris*, *I. histrio* ($2n = 20$), has a 1C genome size of 12.24 pg. *Iris* itself, or at least subgenus *Reticulata* to which *I. histrio* belongs, may be paleopolyploid. The specialized, acaulescent *Galaxia* has the smallest reported genome in Irideae, 1.2 pg, about one-third the size of that in its closest allies (*Moraea* subg. *Moraea*), a puzzling observation.

Genomes are smaller in Ixioideae (Olszewska & Osiecka, 1982; Goldblatt et al., 1984; Goldblatt & Takei, 1993). Using the above correction factor when necessary, 1C genome sizes range from 1.01 pg (or 0.54 pg for the basic genome) in the paleotetraploid *Pillansia* to 0.60 pg in *Gladiolus* (even lower estimates for *Hesperantha* and *Anomatheca* obtained by Goldblatt et al. (1984) are probably not reliable). In *Lapeirousa* genomes ranging from 1.27 to 1.45 pg (corrected for intrageneric polyploidy) were established by Masterson (in Goldblatt & Takei, 1993) using *Nicotiana tabacum* L. as a standard. *Lapeirousia* is evidently unusual in Ixioideae in having genomes as large as those in *Galaxia* (Irideae) and some Tigridieae. Genome sizes reported by Olszewska and Osiecka (1982) in general confirm the above pattern, but as chromosome numbers were not provided for the plants that they studied, corrections for polyploidy are not possible. Their

estimate of a 1C value of 1.1 pg for *Crocosmia* ×*crocosmiiflora* (as *Tritonia*) is, however, consistent with the pattern for Ixioideae. Their reports for *Crocus vernus* (Ixioideae) of 11.56 pg and 2.1 pg for *Iris sibirica* (Iridoideae) may be reversed. *Iris sibirica*, normally $2n = 28$, has much larger chromosomes than *Crocus vernus*, in which diploid numbers of $2n = 8, 10, 12, 16, 18$, and 20 are known (Brighton, 1976).

Genome size sometimes reflects taxonomic relationship, but it is clearly influenced by environmental factors as well, and gross differences between taxa may have little taxonomic significance above species rank. On the other hand, there seems to be a correlation between genome size and species relationships in *Moraea*. In subgenus *Vieusseuxia* ($x = 6$) species have consistently larger genomes than do species of subgenus *Moraea* or the related genus *Dietes* (both $x = 10$). Still larger genomes characterize subgenus *Moraea* and subgenus *Grandiflora* ($x = 6$).

MODES OF NUMERICAL CHANGE

Most generic ancestral base numbers in Iridaceae are relatively high (Tables 2, 3), which suggests an early burst of polyploidy in the evolution of the family or a paleopolyploid origin for the family. Low ancestral base numbers for Tigridieae ($x = 7$), and for *Babiana* and *Zygotritonia* ($x = 7$) and *Syringodea* ($x = 6$) (all Ixioideae), appear to represent paleodiploidy, but we suspect that these base numbers are most likely derived. The latter would be more consistent with their levels of morphological specialization. Neopolyploidy (defined here as intrageneric polyploidy) is common in Northern Hemisphere representatives of the family and is estimated here to be above 60%. For example, in *Gladiolus* 5 polyploid species, 1 of them with diploid races, are known in the 80 species counted from sub-Saharan Africa and Madagascar, but all the 6 to 10 species of the genus that occur in Eurasia and North Africa are tetraploid ($4x$) to dodecaploid ($12x$). Neopolyploidy in African members of the three subfamilies of Iridaceae occurring in sub-Saharan Africa is remarkably low on a world scale. Some 5% of the species of Ixioideae and 10% of Iridoideae are polyploid, and 10% more species of the latter have both diploid and polyploid populations. No species of African Nivenioideae are exclusively polyploid, but 3 species of 24 counted (12%) have diploid and tetraploid races.

Polyploidy appears to be more important in the evolution of South and Central American Iridaceae. Nearly all Central and North American Tigridieae

are tetraploid or hexaploid, including the 10 species of *Tigridia* counted, 2 of 3 species of *Nemastylis* counted, and all 3 species of *Alophia* in the region. One population of a Mexican species of *Tigridia* has a diploid race, and at least two South American species of this genus are diploid. The genera *Fosteria* and *Cobana,* closely allied to *Tigridia,* are apparently exclusively polyploid. In other genera that are moderately well known cytologically, like *Herbertia* and *Cipura,* more than half of the species counted are polyploid. Polyploidy seems equally important in other tribes of Iridoideae in South America, but except for *Sisyrinchium,* the genera are too poorly known cytologically for useful comparisons to be made. For *Sisyrinchium,* subgenus *Sisyrinchium* seems to have over 90% of the species polyploid, while subgenus *Echthronema* has about 75% of the species tetraploid.

Dysploidy (stepwise change in base number) is important in several genera of Iridaceae, and extensive dysploid sequences are described in more detail above for *Crocus, Gladiolus, Lapeirousia,* and *Romulea* (Ixioideae) and *Galaxia* subg. *Eurystigma* and *Moraea* (Iridoideae). Outgroup comparison and/or correlated morphological specializations in dysploid species consititute compelling evidence that decreasing dysploidy has been the dominant or exclusive factor in numerical change in these genera. Less extensive dysploid changes in *Gelasine, Hesperantha, Homeria,* and *Tritonia* should also be regarded as having proceeded from higher to lower base number for the same reasons. In the one species of *Hexaglottis* mentioned above there are examples of both descending and apparent ascending dysploidy. Thus in Iridaceae, all but one of the numerous examples where the direction of dysploid change can be determined, the direction is downward. This is consistent with Jones's (1977) hypothesis that most cases of dysploid change in plant families are downward. Ascending dysploidy is probably a rare phenomenon in natural populations, and arguing from the information about dysploidy in Iridaceae and a few other families, we question whether it has played a significant role in the evolution of any plant group.

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